

The use of photoperiods to provide year round spawning in lumpfish *Cyclopterus lumpus*

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Running title: Manipulation of spawning in lumpfish

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1 **Abstract**

2

3 In order to provide year round spawning broodstock, lumpfish (initial size 746 g and 24.9
4 cm) were reared under four different photoperiod regimes from January 2017 to July 2018.
5 One group was reared under simulated natural photoperiod (LDN, control group) for
6 Tromsø (70°N). The second group was transferred to continuous light (LD240) on 30
7 January 2017 and reared at LD24:0 throughout the trial period. Two compressed and phase
8 advanced photoperiods were also established. Both groups were moved from LDN to
9 LD24:0 on 30 January 2017, and after that reared at compressed natural photoperiods
10 where the annual photoperiod was compressed down to six months (L6) or nine months
11 (L9) for the duration of the study. Spawning time was shifted in both compressed groups
12 during both years of the study. Spawning activity in the second year of the study was higher
13 and followed more closely the expected spawning period in the compressed and the LDN
14 groups. Spawning in the LD240 group was spread out over the experimental period with
15 no distinct peak in spawning. A seasonal and pronounced drop in condition factor was
16 found for females in the L9, L6 and the LDN groups. This post-spawning loss in condition
17 was closely related to the spawning activity of each group. The current findings suggest
18 that photoperiod has a strong influence on the timing of lumpfish maturation and can be
19 used as an efficient and inexpensive tool to secure lumpfish reproduction operations i.e.
20 year-round supply of egg and milt and/or timing with optimal temperature regimes.

21

22 *Keywords:* Lumpfish; compressed and phase-shifted photoperiods; growth; maturation

23

1 **1. Introduction**

2 Lumpfish *Cyclopterus lumpus* L. 1758 is widely distributed across a large area on
3 both sides of the North Atlantic Ocean (Vasconcelos et al., 2004, Bañón et al., 2008;
4 Pampoulie et al., 2014; Jónsdóttir et al., 2018). Natural spawning in lumpfish occurs in
5 spring and early summer (March-June, Davenport, 1985; Mitamura et al., 2012; Kennedy
6 et al., 2015; Kennedy, 2018). Spawning of lumpfish often takes place in shallow sub-tidal
7 waters when temperatures reach around 4°C (Collins, 1976; Daborn and Gregory, 1983).
8 Kennedy (2018) investigated the natural spawning cycle and ovary development of
9 lumpfish. The results showed that ovaries of lumpfish had a wide range of oocyte sizes
10 and that lumpfish is a determinate, batch spawner with ovary development taking at least
11 8 months. They spawn a maximum of two batches per season with a similar number of
12 eggs in each batch. Lumpfish were documented as spawning over a 4-month period (weeks
13 13-27, March – July), but it is likely that spawning may occur over a greater period.

14 Recently the lumpfish has been suggested as a cold-water cleaner fish for removal
15 of sea lice from Atlantic salmon, *Salmo salar* (Imslund et al., 2014 a-c; 2015a-b). Interest
16 in use of hatchery reared lumpfish has increased rapidly concurrent with the species use
17 as biological delouser on Atlantic salmon. There is; therefore, a need for year-round
18 production of lumpfish juveniles. To reach that goal development of methods for the
19 management of sexual maturation and spawning are necessary. As a first step for
20 developing methods to manage sexual maturation Imslund et al. (2018) exposed groups of
21 juvenile lumpfish previously reared under simulated natural photoperiod to continuous
22 light from April to January and from April to April the subsequent year followed by 8
23 week decline in hours of light from 24 to 4 hours (autumn signal) and subsequent 8 week

1 rise from 4 to 24 hours (spring signal). In both groups spawning was seen 3-6 months after
2 the onset of short autumn-short spring photoperiodic signal whereas no spawning was
3 found in the control group reared at simulated natural photoperiod. These findings indicate
4 that spawning control in lumpfish is possible through manipulation of photoperiods.

5 In temperate regions, teleost reproduction follows a seasonal cycle, which is
6 synchronized by several environmental factors such as photoperiod (Wang et al. 2010; Cyr
7 et al., 2018). These external factors influence/synchronize endogenous rhythms which
8 result in a spawning synchronicity within populations and increase offspring survival
9 (Bromage et al., 2001; Taranger et al., 2010; Cyr et al., 2018). Photoperiod control of the
10 reproductive process has been successfully applied to broodstock to alter the phase of the
11 annual sexual cycles and hence the spawning time in a range of fish species (e.g. Taranger
12 et al., 2010). A range of studies demonstrate that photoperiod manipulation can be an
13 effective tool to control, and synchronize, maturation in farmed fish, e.g. Atlantic salmon
14 (Oppedal et al., 2006), Arctic charr, *Salvelinus alpinus* (Gunnarsson et al., 2012), Atlantic
15 cod, *Gadus morhua* (Norberg et al., 2004; Imsland et al., 2013a), Atlantic halibut,
16 *Hippoglossus hippoglossus* (Norberg et al., 2001; Imsland et al., 2009), turbot,
17 *Scophthalmus maximus* (Imsland et al., 2003, 2013b; Imsland and Jonassen, 2003),
18 Senegalensis sole, *Solea senegalensis* (Garcia-Lopez et al., 2006), common dentex, *Dentex*
19 *dentex* (Pavlidis et al., 2001) and lumpfish (Imsland et al., 2018). However, the
20 effectiveness of photoperiod protocols differs among species and appears also to be
21 modulated by other factors such as age, feeding, body size, adiposity and the stage of
22 maturation of the fish (Taranger et al., 1999, 2010; Oppedal et al., 2006; Taylor et al.,
23 2008).

1 In salmonids (autumn spawners) long photoperiods or continuous light early in the
2 season are believed to phase advance circannual rhythms that control the seasonal timing
3 of onset and completion of puberty, whereas long photoperiods or continuous light from
4 midsummer onwards delay such rhythms (Bromage et al., 2001; Taranger et al., 2010). For
5 spring spawning species as Atlantic cod continuous light treatment has been found to arrest
6 or delay pubertal development when applied from around mid-summer and onwards
7 (Hansen et al., 2001; Davie et al., 2003, 2007a; Karlsen et al., 2006; Imsland et al., 2013a).
8 A similar delay of maturation by applying continuous light one year before first maturity
9 has been found in the Atlantic halibut (Imsland et al., 2009). The effect of compressed and
10 phase-shifted photoperiod is less documented but in general such treatment seems to
11 advance spawning allowing for synchronizing spawning time for year round production of
12 gametes (Bromage et al., 2001; Morehead et al., 2000; Norberg et al., 2004; Guerrero-
13 Tortolero et al., 2010; Newman et al., 2010; Cyr et al., 2018).

14 At present only one published study exists on the effect of continuous light or other
15 light regimes on growth in lumpfish (Imsland et al., 2018). Here, exposure of lumpfish to
16 continuous light in spring for 9-12 months followed by an autumn-spring signal stimulated
17 somatic growth especially in females. The growth enhancing effect of continuous light
18 lasted for approximately six months in females compared to one month in the males. In
19 other marine species, there are indications that exposure to continuous light during the
20 juvenile stage may significantly affect subsequent growth and thereby age at maturity
21 (Imsland and Jonassen, 2003, 2005; Imsland et al., 2009, 2013a-b). However, in some cases
22 prolonged exposure to continuous or extended light regimes may reduce growth and food
23 conversion efficiency (e.g. Stefánsson et al., 2002), so the period of extended or continuous

1 light must be synchronized with the internal rhythms of the fish and the season in order to
2 achieve increased growth and/or lower maturity. Based on findings from other marine
3 species and the recent study of Imsland et al. (2018) we hypothesize that rearing juvenile
4 lumpfish at continuous light will enhance growth during the late juvenile phase. If
5 maturation is triggered at a certain size threshold as seen in many teleosts (Imsland et al.,
6 1997a) the enhanced growth will alter the age at 1st maturation in lumpfish.

7 The rationale behind the chosen light regimes in the current trial, was to investigate
8 possible effect of phase advanced and compressed photoperiods on growth and maturation
9 in lumpfish. Accordingly, a study was performed where 1+ juvenile lumpfish (initial
10 weight 746 g) were reared under simulated natural photoperiod for Tromsø, (LDN, control
11 group) with expected first spawning in spring 2017 based on the natural spawning cycle
12 for the species (Collins, 1976; Daborn and Gregory, 1983; Kennedy, 2018). In addition,
13 there were three groups exposed to continuous light from late January 2017, two of those
14 (L6 and L9) were thereafter reared on phase advanced compressed annual photoperiod (12
15 months cycle compressed to 6 and 9 months, respectively) and the third group reared under
16 continuous light (LD240) throughout the trial period.

17 The objective of this study was to investigate if it is possible to change the annual
18 spawning season in lumpfish by rearing the fish under phase advanced and compressed
19 photoperiods. A second objective was to investigate how rearing at continuous light affects
20 the growth properties of lumpfish during the late juvenile phase and whether 24L brings
21 spawning of the individual fish out of synchrony within the group and with the normal
22 season. Based on the effect of photoperiod on controlling maturity and the effect of phase
23 advancing and compressing photoperiods in other species we predict that spawning time

- 1 will shift in the compressed photoperiods with spawning starting once hours of light per
- 2 day in the artificial spring reach 8-10 h and continuing for 3-5 months.
- 3

1 **2. Materials and Methods**

2

3 *2.1 Pre-experimental protocol*

4 Sexually mature wild lumpfish (10 females and 2 males) were caught by local
5 fishermen in gill nets at Hekkingen, Sommarøy, Troms County, Norway during
6 September-October 2015. The fertilized eggs were incubated at 8.5-9.7°C at Akvaplan-
7 niva research station at Kraknes (APN-K) and later transferred to Senja Akvakultursenter,
8 Senja, Troms County where they hatched in December 2015 and were reared in 8-10 m³
9 tanks at 10-11°C. In June 2016 1500 lumpfish juveniles were transported back to APN-K
10 and reared at 8-10°C and simulated natural photoperiod (LDN) for Tromsø (N 69° 40') to
11 experimental start-up in January 2017. The juveniles were initially fed with Gemma Micro
12 (150 -500 µm, Skretting, Norway). After 30 days, the juveniles were fed with 500-800 µm
13 dry feed pellets (Gemma Wean Diamond, Skretting, Norway). After approximately 120
14 days the juveniles were fed with Gemma Wean diamond 2.0 mm (Skretting AS, Stavanger,
15 Norway) and pellet size increased according to size following the producers
16 recommendation.

17

18 *2.2 Experimental set-up and rearing conditions*

19 Two tanks were reared under simulated natural photoperiod for Tromsø prior to
20 start of the experiment in January 2017. On 30 January 2017 four experimental groups (Fig.
21 1) with a mean (\pm SD) weight of 746 g (\pm 175) and length 24.9 cm (\pm 1.6) were established.
22 One group remained on LDN (control group) and one group was transferred to continuous
23 light (LD240) and reared under this regime throughout the trial period. Two phase

1 advanced and compressed photoperiods were also established on 30 January. Both groups
2 were moved to continuous light and after that reared at compressed natural photoperiods
3 where the annual photoperiod was compressed down to six months (L6) or nine months
4 (L9). The trial was terminated on 12 July 2018.

5 On 19-21 June 2017 all lumpfish (N=300) with an average (\pm SD) weight of 1267
6 g (\pm 324 g) and length of 28.01 cm (\pm 3.2 g) (were anaesthetized (Finquel® 150 mg L⁻¹)
7 and tagged intraperitoneally with a Trovan® Passive Integrated Transponder and
8 distributed among eight 12 m³ tanks at APN-K with 37-38 fish in each tank. Light in all
9 tanks was supplied using two 18W fluorescent daylight tubes positioned in the centre of
10 the tank-cover. Photoirradiance at the tank bottom was approximately 15.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

11 The fish were reared under ambient water conditions (Fig. 2) with minimum
12 temperatures around 3.0°C in February and maximum around 9.0°C in September-October
13 and annual average temperature of 5.8°C. Salinity was around 34.1 ppt. throughout the
14 study period. Dissolved oxygen ranged between 8.9 mg l⁻¹ and 11.1 mg l⁻¹ during the trial
15 period. The fish were fed to satiation with a commercial formulated feed (4-7 mm,
16 Skretting Amber Neptun, Stavanger, Norway) containing 16% fat and 52% protein during
17 light hours in the LDN.

18

19 *2.4 Growth and maturation*

20 All fish were individually weighted and their length measured at the following dates:
21 30-31 January 2017, 20-21 June 2017, 15-16 November 2017, 27-28 March 2017, 30-31
22 May 2017, 10-12 July 2018. Specific growth rate (SGR) of individual lumpfish was
23 calculated according to the formula of Houde and Schekter (1981):

1
$$\text{SGR} = (e^g - 1) \times 100$$

2 where $g = (\ln(W_2) - \ln(W_1)) / (t_2 - t_1)$ and W_2 and W_1 are weights on days t_2 and t_1 ,
3 respectively.

4 The condition factor (K) of individual lumpfish (calculated at each sampling interval)
5 was defined as:

6
$$K = 100 * W / L^3$$

7 where W is the weight (g) of the fish and L the corresponding total length (cm).

8 All fish were sexed as it is possible to sex lumpfish based on skin coloration from
9 early juvenile age (Davenport and Bradshaw, 1995). From beginning of the trial all fish
10 were checked regularly for sexual maturation by examining external morphology. Fish in
11 later stages of their sexual maturation were gently hand-stripped. Each experimental tank
12 was examined daily and any eggs removed. When in the ovary-oviduct, lumpfish eggs are
13 invariably rose pink in colour, but after discharge to the environment they change to a
14 variety of yellow, green, purple, violet, blue and grey colours each mass being of fairly
15 homogenous colour (Davenport, 1985). Accordingly, it was possible to distinguish
16 individual spawnings in the tank based on coloration of the eggs sampled (Davenport,
17 1985; Armand Nes, Akvaplan-niva, Kraknes research station, pers. comm.). The fish were
18 slaughtered after termination of the trial in July 2018 and sex of all individuals confirmed
19 and all fish categorized into eight groups with the sampling size in each group as follows:
20 L6-males (N=28), L6-females (N=47); L9-males (N=31), L9-females (N=44); LND-males
21 (N=32), LND-females (N=43); LD240-males (N=30), LD240-females (N=45).

22

23 *2.6. Statistics*

1 All statistical analyses were conducted using Statistica™ 13.3 software. A
 2 Kolmogorov-Smirnov test (Zar, 1984) was used to assess for normality of distributions.
 3 The homogeneity of variances was tested using the Levene's F test (Zar, 1984 Data on
 4 mortality and spawning activity was tested with a χ^2 test with the LDN group as expected
 5 value. A three-way nested analysis of variance (ANOVA, Searle et al., 1992) where
 6 replicates are nested within photoperiod group and sex was applied to calculate the effect
 7 of different photoperiods and sex on mean weights, condition factor and specific growth
 8 rates. The model equation of the nested ANOVA had the form:

$$9 \quad (1) \quad X_{ijk} = \mu + \alpha_i + \beta_j + \gamma_{ij} + C_{ijk} + \varepsilon_{ijkl}$$

10 where μ is the general level; α_i is the photoperiod effect; β_j is the sex effect; γ_{ij} is the
 11 interactive effect between photoperiod and sex; C_{ijk} is the contribution caused by replicate
 12 (tank) k in photoperiod i and sex j and ε_{ijkl} is the error term. We assume that $\varepsilon_{ijkl} \sim$ Normal
 13 distributed $(0, \sigma^2)$. Possible changes over time in condition factor was tested with a linear
 14 regression.

15 Mean individual growth trajectories were analysed using a growth curve multivariate
 16 analysis (GCM) of variance (MANOVA) model (Timm, 1980; Chambers and Miller,
 17 1995). The model equation of the GCM had the form:

$$18 \quad (2) \quad \mathbf{Y} (n \times p) = \mathbf{X} (n \times q) \mathbf{B} (q \times p) + \mathbf{E} (n \times p)$$

19 Where $\mathbf{Y} (n \times p)$ are the growth at age vectors

$$20 \quad (3) \quad \mathbf{y} = (y_1, y_2, \dots, y_p)$$

21 for each p (age) measurements on n individual fish; $\mathbf{X} (n \times q)$ is the design matrix or the set
 22 of extraneous variables measured for each individual, i.e., $q = \text{age}_i + \text{photoperiod regime}_j$ (j
 23 = L6; L9; LDN; LD240) + sex_k ($k = \text{female; male}$) + replicate_j ($j = \text{replicate a; replicate b}$);

1 **B** ($q \times p$) is the matrix of parameters estimated by the model; **E** ($n \times p$) is the matrix of
2 deviations for each individual from the expected value of $\mathbf{Y} = \mathbf{XB}$

3 Significant differences revealed in MANOVA or ANOVA were followed by Student-
4 Newman-Keuls (SNK) post hoc test to determine differences among experimental groups.

5 A significance level (α) of 0.05 was used if not stated otherwise. In cases with non-
6 significant statistical tests, power ($1-\beta$) analysis was performed in Statistica using $\alpha = 0.05$.

7

1 **3. Results**

2 *3.1 Growth and mortality*

3 A total of 37 (12%) fish died during the experiment. The mortality did not vary among
4 the groups ($\chi^2 \leq 2.7$, $p > 0.10$) and occurred mainly during the spawning period in each
5 experimental group. The overall initial mean weight (SD) was 746 (175) g and did not
6 differ (three way nested ANOVA, $p > 0.6$, Power $(1 - \beta) > 0.7$, Fig. 3) among sex and
7 photoperiod groups. From June 2017 and throughout the study all male groups displayed
8 lower mean weights (SNK test, $p < 0.05$, Fig. 3) compared to the females. Significant effect
9 of photoperiod (three way nested ANOVA, $F_{3, 254} = 5.1$ $p < 0.05$) was seen from November
10 to March as LDN males were larger than the three other male groups (SNK test, $p < 0.05$).
11 A significant interactive effect of photoperiod and sex (three way nested ANOVA, $F_{3, 216}$
12 $= 4.7$, $p < 0.05$) was seen in May 2018 as female LD240 were largest of the four female
13 groups whereas LD240 males were the smallest of the males (Fig. 3). No significant
14 differences between the photoperiod groups within each sex was seen at the termination of
15 the trial (SNK test, $p > 0.30$).

16 The fish reared on the different photoperiod regimes differed in their growth patterns,
17 as the GCM analyses revealed differences between the individual growth trajectories of the
18 photoperiod regimes (MANOVA_(PHOTOPERIOD), Wilk's $\Lambda_{12, 262} = 0.61$, $p < 0.001$, Fig. 4),
19 sex (MANOVA_(SEX), Wilk's $\Lambda_{4, 99} = 0.65$, $p < 0.001$) and interaction between photoperiod
20 and sex (MANOVA_(PHOTOPERIOD X SEX), Wilk's $\Lambda_{12, 262} = 0.72$, $p < 0.001$). Growth rates
21 varied between the sexes from onset of the trial (three ways nested ANOVA, $p < 0.05$),
22 whereas photoperiod effects were found from June 2017 to May 2018, and interactive effect
23 of sex and photoperiod between June and November 2017 (Fig. 4). The L6 females

1 displayed the highest growth of all groups between June and November (SNK post hoc test,
2 $p < 0.01$). Average negative growth (weight loss) was seen for the LDN females and males
3 from March 2018 onwards as well as for females in the L6 group and females and males in
4 the LD240 group during the final period of the trial (Fig. 4).

5 Initial condition factor (K) did not vary between the experimental groups (three way
6 nested ANOVA, $P > 0.3$, $(1 - \beta) > 0.7$, Fig. 5). The effect of photoperiod on K was
7 significant in May 2018 as the females in the LD240 group displayed higher K (SNK test,
8 $p < 0.05$) compared to the LDN and L9 female groups. A significant interactive effect of
9 photoperiod and sex (three way nested ANOVA, $p < 0.05$) was seen in in November 2017
10 and July 2018 as female L6 (November) and LD240 (July) had the highest K of the female
11 groups but no such trend was seen in the males at these dates (Fig. 5). The K sank
12 significantly from June to November for the L9 females (linear regression, $\beta = -0.31$, $p <$
13 0.001 , Fig. 5), from November onwards for the L6 females (linear regression, $\beta = -0.29$, $p <$
14 0.001) and from March to July 2018 for the LDN females (linear regression, $\beta = -0.41$, $p <$
15 0.001).

16

17 *3.2 Maturation*

18 Spawning colouration and running milt was seen for males in all four photoperiod
19 groups from June 2017 onwards. In the females, spawning time varied between the
20 photoperiod groups (Fig. 6, Table 1). Spawning in the LDN group was about 3 months
21 delayed in relation to expected spawning time in 2017, but spawning increased for this
22 group in 2018 and was observed between March and July in line with expected spawning
23 time (Fig. 6). In both phase advanced compressed groups spawning took place around the

1 expected spawning periods in both years of the trial. Few females in the L6 group spawned
2 in June and July 2017 (Table 1), but higher spawning activity was seen in this group
3 between January and May in 2018 according to their spring-summer photoperiod. High
4 proportion of spawning females was found in the L9 group between July and September
5 2017 and from February to June in 2018, according to their spring photoperiod. Spawning
6 in the LD240 female group occurred sporadically throughout the trial period and did not
7 show any apparent pattern. Spawning activity was significantly higher in the L9 group
8 compared to the control group (LDN) during spring 2018 ($\chi^2 = 4.0$, $p < 0.05$, Table 1) and
9 significantly lower for the LD240 group compared the L9 and LDN groups during 2018
10 ($\chi^2 > 5.1$, $p < 0.05$). Spawning activity was marginally lower in the L6 group compared to
11 the L9 group during summer 2017 ($\chi^2 = 3.8$, $p < 0.05$).

12

13

1 **4. Discussion**

2

3 *4.1 Maturation*

4 The efficiency of photoperiod manipulation as a tool for regulating reproduction in
5 lumpfish is demonstrated by the shift in spawning cycle caused by the altered light regimes.
6 Expected spawning times based on earlier trials and lumpfish natural spawning time in the
7 LDN group is between March-June (Davenport, 1985; Mitamura et al., 2012; Kennedy et
8 al., 2015; Kennedy, 2018) whereas spawning commenced in the LDN group in July 2017
9 i.e. 3-5 months delayed. An explanation for the delayed response could be that the
10 developmental stage or size threshold needed to respond to photoperiod was not reached
11 until summer 2017. Such size related threshold of maturation has previously been indicated
12 by Imsland et al. (2018) where female lumpfish spawned at approximately 1.5 kg. This size
13 was reached in June-July 2017 concomitant with onset of spawning in the LDN group.
14 Spawning activity in the second year of the study was higher and followed more closely
15 the expected spawning period in the compressed and the LDN groups.

16 Earlier studies have shown that phase advanced and compressed natural photoperiods
17 treatment seem to advance spawning allowing for synchronizing spawning time for year
18 round production of gametes. Morehead et al. (2000) reared sexually mature striped
19 trumpeter *Latris lineata* on either a 12-month cycle of ambient temperature (9-18°C) and
20 photoperiod, or a 9-month compressed temperature and photoperiod cycle and found that
21 the compressed cycle advanced spawning by 1 and 4 months during consecutive seasons.
22 Norberg et al. (2004) compressed the annual photoperiod cycle of Atlantic cod into 6 or 9
23 months, held at 12 months, or extended to 18 months, in each case followed by one 12-

1 month cycle (termed 6+12, 9+12, 12+12, and 18+12, respectively). Photoperiod alterations
2 caused shifts in the cyclic patterns of plasma calcium, sex steroid, and thyroid hormones,
3 and also produced correlative changes in the timing of spawning. Initial spawning was
4 advanced in the compressed (6+12) photoperiod group, followed by further advancement
5 in the timing of the second spawning. Conversely, spawning was delayed in the 18+12
6 group. Guerrero-Tortolero et al. (2010) compressed the yearly photoperiod down to 3
7 month period in yellowtail snapper, *Lutjanus argentiventris* and achieved spawning, in this
8 group during winter approximately 6 months prior to the natural spawning season. Newman
9 et al. (2010) investigated the effect of phase advancing the photoperiod for three months in
10 Murray cod, *Maccullochella peelii peelii*, and found that maturation was advanced for
11 three-four months. In common wolffish, *Anarhichas lupus*, and spotted wolffish,
12 *Anarhichas minor* fish subjected to a 8-month compressed photoperiod spawned 2-6
13 months earlier than the controls (Cyr et al., 2018). Overall, present data are in line with the
14 published earlier findings, showing that many teleost species will readily react to phase
15 advanced and compressed photoperiod cycle by advancing the annual timing of spawning.
16 However, the effect is also dependent on the prior maturation stage of the fish and other
17 external factors such as temperature.

18 As the fish were reared under ambient temperature in the present trial it may also be
19 speculated if temperature had a confounding or masking effect for spawning in lumpfish.
20 Notable the minimum temperatures in the second year of the trial were about 2°C lower
21 (2.7°C vs- 4.8°C). This was due to colder sea water conditions near the water inlet for the
22 experimental station. Despite these low temperatures spawning was not delayed in the
23 experimental groups during this period of low temperature. In nature spawning of lumpfish

1 often takes place in shallow sub-tidal waters when temperatures reach around 4°C (Collins,
2 1976; Daborn and Gregory, 1983) and current data indicate that temperatures as low as 2.7-
3 3.3°C for a 4-5 week period in early spring does seemingly not interfere with the natural
4 spawning progression of lumpfish. Natural spawning in lumpfish occurs in spring and early
5 summer (April-July, Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015) when
6 low sea water temperatures in line with those seen in the current study can be expected.

7 Lower spawning activity was seen in the L6 compared to the L9 group in the first
8 half of the study (2017). A possible explanation could be that the phase advanced
9 compressed photoperiodic signal from winter to summer solstice that naturally is 6 months
10 long was compressed to 3 months. Although the fish can perceive the light signals it may
11 still need more than 3 months to finalize the maturation process. This could explain the
12 higher spawning activity in the L9 group during this period where the same photoperiodic
13 signal was 4.5 month. Overall, our findings indicate that exposure to phase advanced
14 compressed natural photoperiod signal can be used to control the spawning time in
15 lumpfish. Although the female lumpfish display a positive response to photoperiod in
16 relation to growth it is more unclear how the females utilize photoperiod signal to
17 synchronize the spawning. It may be speculated that lumpfish do not synchronize for a
18 narrow spawning season as the natural spawning period extends from early spring to
19 autumn (Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018).

20 Rearing lumpfish under continuous light resulted in infrequent and non-rhythmic
21 spawning, i.e. free-running, throughout the study period. It is well established that
22 continuous light modulates the endocrine regulations and regulatory pathways from the
23 brain-pituitary-gonad axis (Taranger et al., 2010) thereby modulating the onset of puberty.

1 Rearing fish without photoperiod cue as done under continuous light may also lead to
2 absence of the melatonin rhythm (Davie et al., 2007b; Bayarri et al., 2009), which in turn
3 can alter the circadian variations of reproductive hormones causing irregularities in the
4 reproductive process (Bayarri et al., 2009). Under continuous light fish may enter into a
5 free running rhythm (as seen in present study) or block or delay the onset of gametogenesis
6 (Karlsen et al., 2014). However, the response towards continuous light can be stage-
7 dependent (Hansen et al., 2001). Such stage-dependent response towards continuous light
8 was seen in the study of Imsland et al. (2013a) where maturation in juvenile Atlantic cod
9 was postponed 6-12 months in groups exposed to continuous light during juvenile stages
10 (600-800 g) whereas later exposure (> 1000 g) did not have any effect on maturation.
11 Findings for Atlantic salmon reared in sea cages have also highlighted the importance of
12 the timing of exposure to continuous light in the control of maturation (Hansen et al., 1992;
13 Porter et al., 1999; Taranger et al. 1999), as exposure to continuous light out of phase with
14 the natural light cycle, i.e. during winter, resulted in fewer fish reaching maturation.
15 Delayed maturation in turbot exposed to continuous light during the juvenile stage has also
16 been documented for first time spawners (Imsland et al., 1997a-b). This may indicate that
17 the timing of continuous light exposure is important with respect to subsequent maturation
18 and that the decision to mature is a gated rhythm (Taranger et al., 1998; Bromage et al.,
19 2001). It is possible that the “gate open” position can vary between species (Imsland et al.,
20 2003) according to their natural spawning season and timing of the initiation of the
21 maturation process. This could help to explain the different effects of exposure to
22 compressed photoperiods on timing of sexual maturation in different species (Norberg et
23 al., 2004; Cyr et al., 2018 present study).

1

2 *4.2 Growth*

3 In the present study, exposure of lumpfish to compressed photoperiods changed the
4 growth pattern compared to the control group and affected age at first maturity in females.
5 Growth in the males in all four photoperiod groups was very slow or halted once they
6 reached approximately 1200 g (around 28 cm). Previous research has demonstrated the
7 sexual dimorphism in size (Imsland et al., 2018) and skin colouration of lumpfish (Goulet
8 et al., 1986). Mature females range from 35-45 cm and are often bluish grey or green in
9 colour, while males are 17-38 cm and display nuptial colour of pink, orange and deep red
10 (Daborn and Gregory, 1983; Davenport, 1985). Sexual maturation influences the growth
11 differently between the sexes (Imsland et al., 1997b; Imsland and Jonassen, 2005). First
12 signs of maturation in the males were apparent from 600 g resulting in stagnation of growth
13 as previously seen in Imsland et al. (2018), whereas the females started to mature at a much
14 larger size (approx. 1500 g). These findings are in line with data from wild lumpfish where
15 males mature one year prior, and at a much smaller size, compared to females (Hedeholm
16 et al, 2014). For the females growth increased with increasing day-length. During summer
17 and autumn of 2017 the L6 female group displayed higher growth compared to other female
18 groups. Part of the explanation could be that the higher maturation seen in the L9 and LDN
19 groups as maturation in lumpfish will slow or halt the growth (Hedeholm et al., 2014). The
20 stunted growth seen for both sexes in the LDN and LD240 groups as well as for L6 females
21 during the final stages of the trial may reflect the energy costs of reproduction as confirmed
22 in previous photoperiod trials in other marine teleosts (Karlsen et al., 2006; Imsland et al.,
23 2003, 2009, 2013a-b; Taranger et al., 2010).

1 The seasonal and pronounced drop in condition factor found for females in the L9,
2 L6 and the LDN groups (Fig. 4) suggests a post-spawning loss in condition as it was closely
3 related to the spawning activity of each group (Fig. 6). In nature seasonal changes in growth
4 have been seen in juvenile lumpfish (Moring, 2001), with higher K in autumn prior to
5 spawning period compared to the post-spawning period during summer. Studies on other
6 marine species in the northeast Atlantic have shown similar seasonal change in K with
7 lower K during winter (Haug et al., 1989; Imsland et al., 1995). The results from the present
8 study indicate seasonal changes in growth and condition factor in lumpfish, in accordance
9 with earlier findings on juvenile lumpfish in nature.

10

11 **5. Conclusions**

12 Photoperiod has a strong influence on the timing of lumpfish maturation and can be used
13 as an efficient and inexpensive tool to secure lumpfish reproduction operations. Males in
14 all experimental groups reached maturation at 600–800 g independent of photoperiod
15 regime indicating that final maturation started prior to the photoperiod treatment in present
16 study. Spawning time was shifted in both compressed groups during both years of the study
17 indicating that a year round supply of eggs can be achieved in commercial operations of
18 lumpfish production. Spawning in the LD240 group was spread out over the experimental
19 period with no distinct peak in spawning.

20

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3

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6

7

1 **Figure captions**

2

3 **Fig. 1.** Photoperiods applied in the experiment. The control group was reared at LDN
4 (Simulated natural photoperiod of Tromsø, N-Norway, 69°40'N) throughout the
5 experimental period (30 January 2017 – 12 July 2018). The L6 and L9 groups were
6 transferred to continuous light on 30 Jan. 2017 and then reared under a 6 and 9 month,
7 respectively, compressed and phase shifted LDN regime throughout the trial. The LD240
8 group was reared under continuous light from 30 Jan. 2017 onwards.

9

10 **Fig. 2.** Temperature profile during the experimental period.

11

12 **Fig. 3.** Mean weight of individually tagged male (M) and female (F) lumpfish reared at
13 four different photoperiods. Vertical lines indicate SE. Solid lines=females; broken
14 lines=males. Squares=L6; triangles=L9; circles=LD240; diamonds=LDN. Capital letters
15 at top of the plot indicate significant effect (three way nested ANOVA, $P < 0.05$) of
16 photoperiod (P), sex (S) and interaction between photoperiod and sex (PxS), N.N., not
17 significant.

18

19 **Fig. 4.** Growth rates of individually tagged male (M) and female (F) lumpfish reared at
20 four different photoperiods. Vertical lines indicate SE. Capital letters below plot indicate
21 significant effect (three way nested ANOVA, $P < 0.05$) of photoperiod (P), sex (S) and
22 interaction between photoperiod and sex (PxS), .N.S., not significant.

23

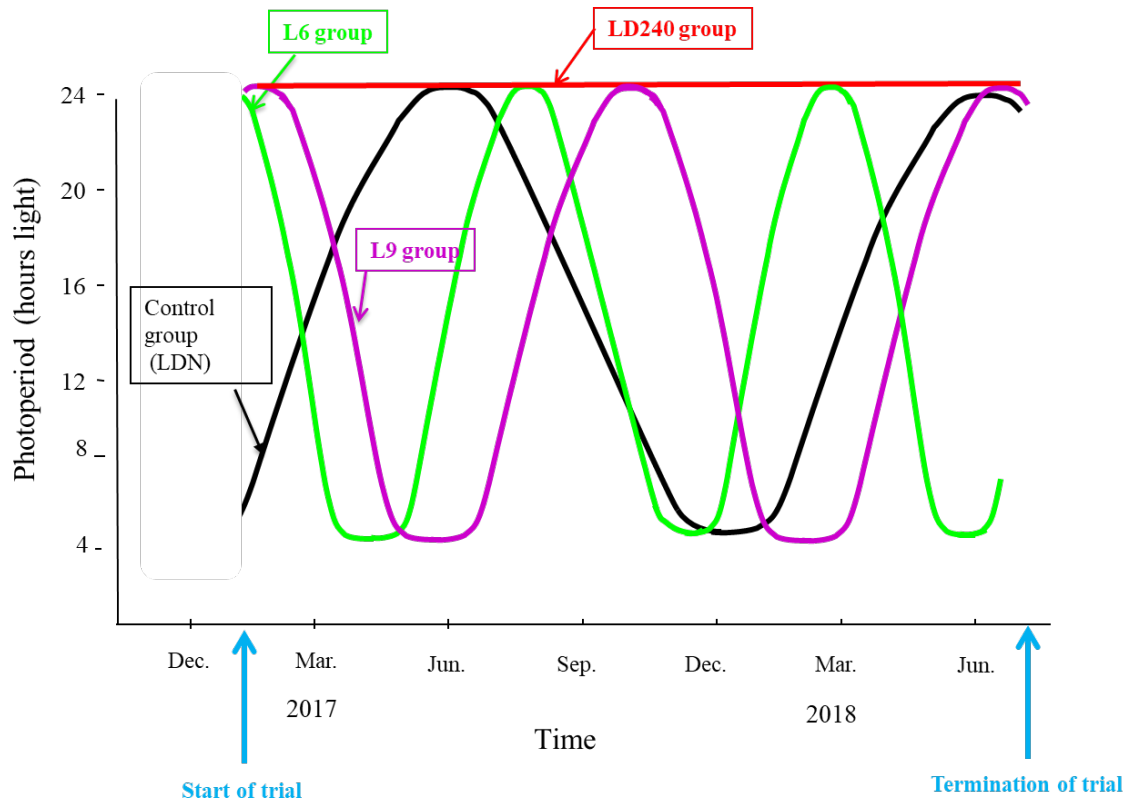
1 **Fig. 5.** Mean condition factor of individually tagged male (M) and female (F) lumpfish
2 reared at three different photoperiods. Vertical lines indicate SE. Whole lines=females;
3 broken lines=males. Squares=L6; triangles=L9; circles=LD240; diamonds=LDN. Capital
4 letters at top of the plot indicate significant effect (three way nested ANOVA, $P < 0.05$) of
5 photoperiod (P), sex (S) and interaction between photoperiod and sex (PxS), N.N., not
6 significant.

7

8 **Fig. 6.** Individual spawning time for female lumpfish reared at four different photoperiods.
9 Spawnings are marked with different symbols for each group: squares=L6; triangles=L9;
10 circles=LD240 and diamonds=LDN. Expected spawning times based on earlier trials and
11 lumpfish natural spawning time in the LDN group (March-June, Davenport, 1985;
12 Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018) and for similar light
13 conditions (i.e. spring to early summer) in the L6 and L9 groups are indicated in the vertical
14 boxes.

15

16

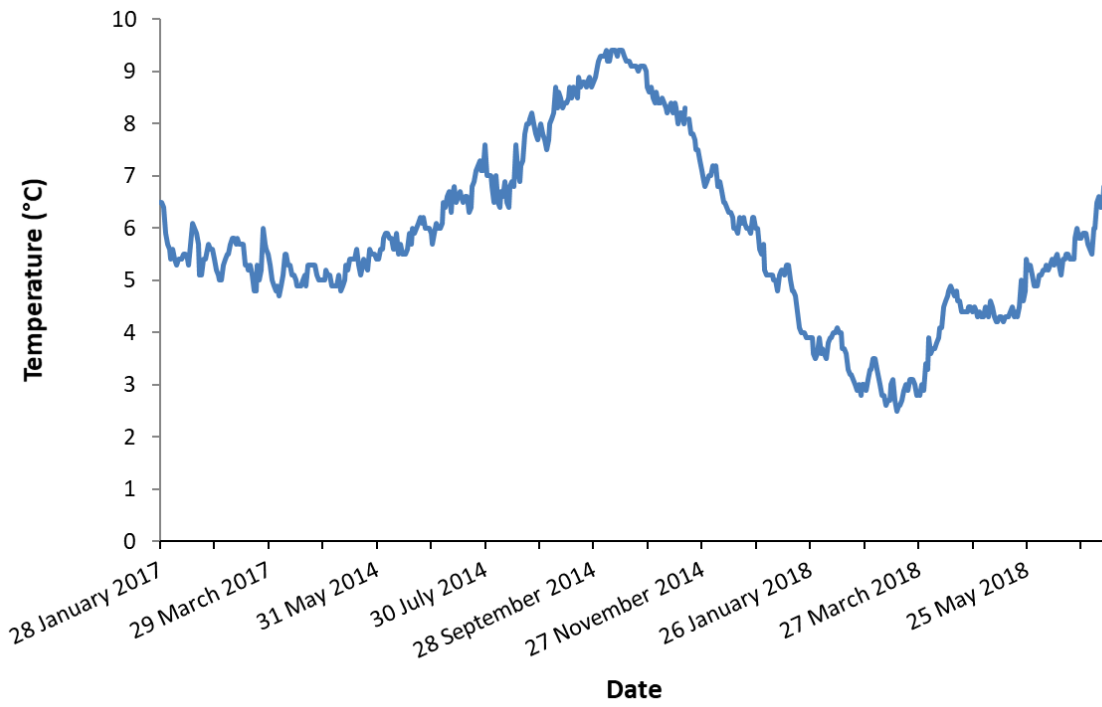


1

2 **Fig. 1.** Imsland et al.

3

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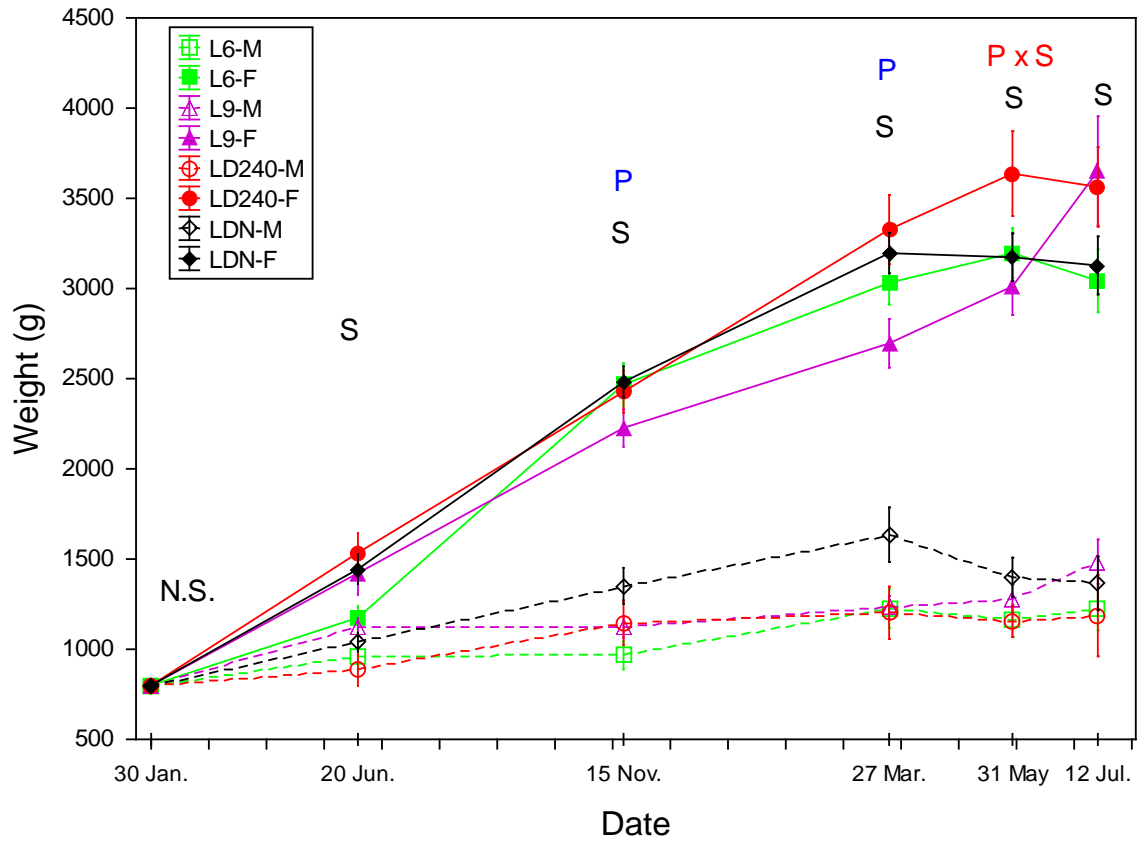
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3 **Fig. 2.** Imsland et al.

4

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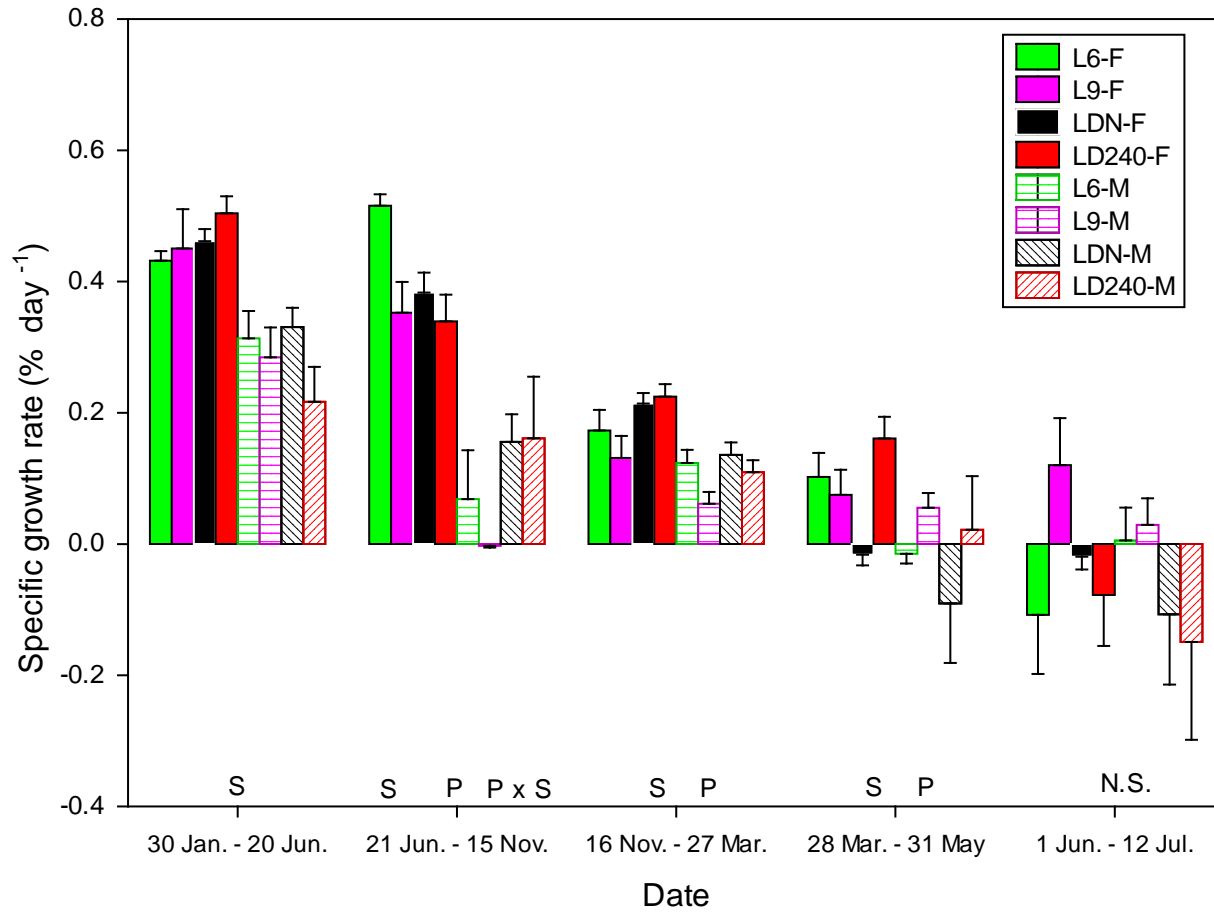
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4 **Fig. 3.** Imsland et al.

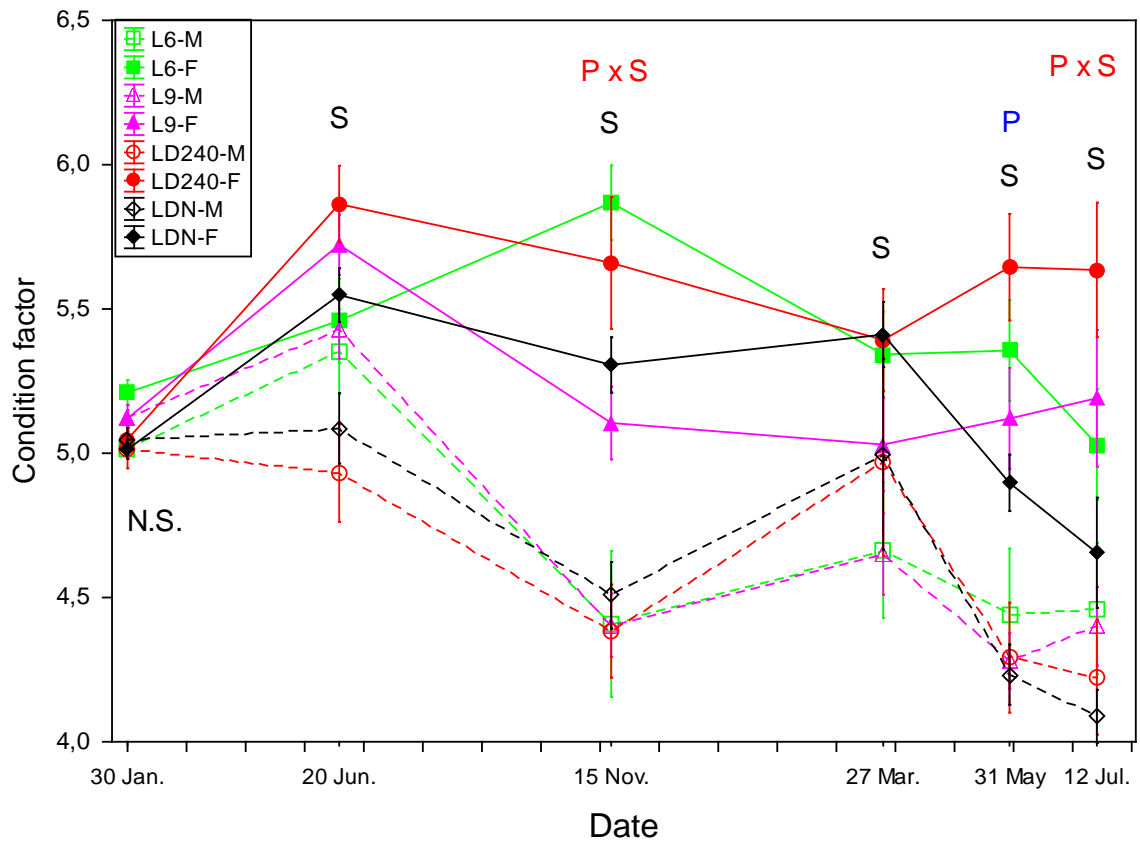
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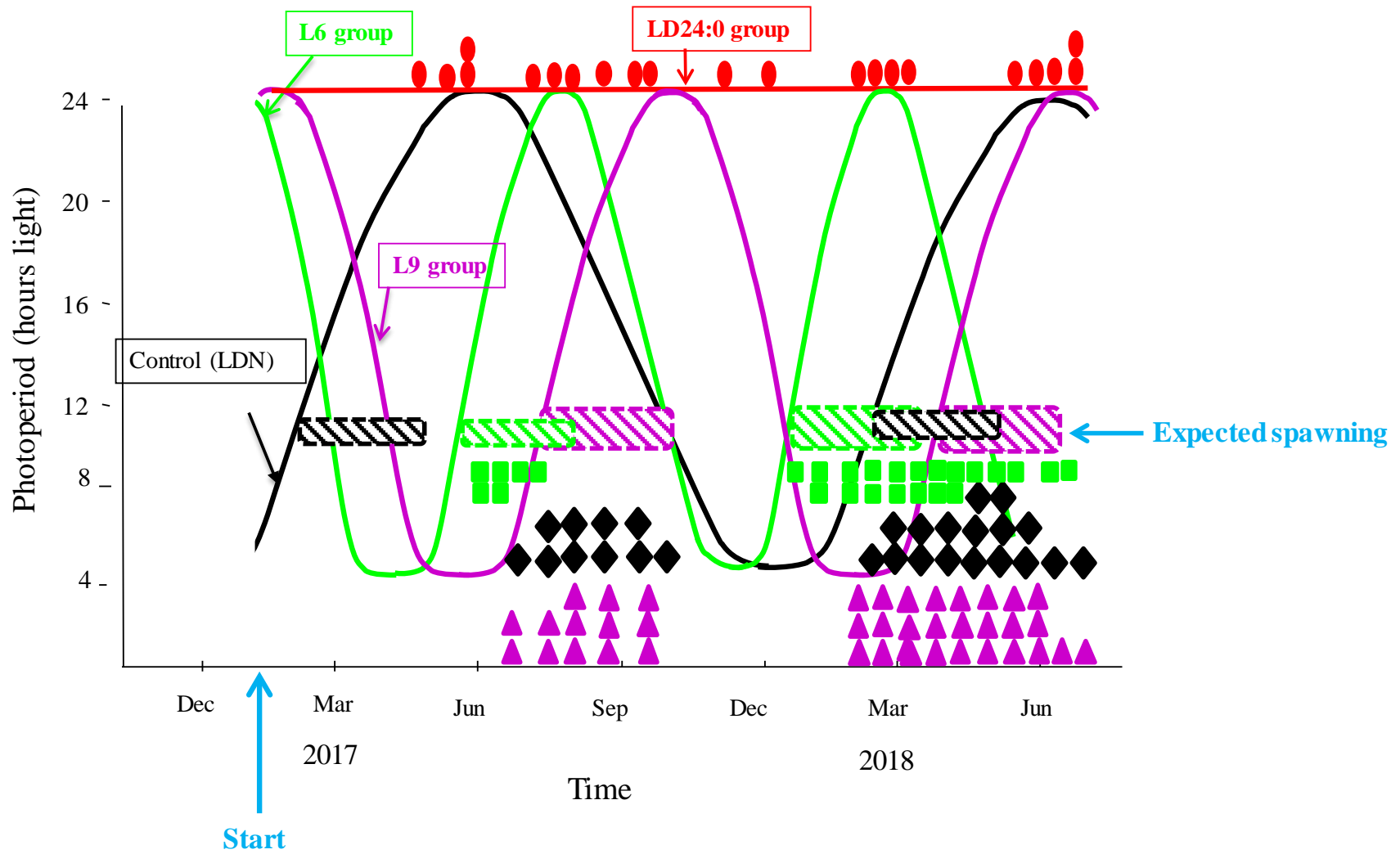
3 **Fig. 4.** Imsland et al.

1



2

3 **Fig. 5.** Imsland et al.



1
2 **Fig. 6.** Imsland et al.

- 1 **Table 1.** Overview of the experimental photoperiods, size of fish at start and end, spawning period (# of egg batches) and
- 2 temperatures in the spawning period for both experimental years.

Experimental group	Size (g)				Female spawning period (# of egg batches)		Temperature (°C) in spawning period	
	Males		Females		2017	2018	2017	2018
	Start	End	Start	End				
LDN	753	1375	775	3140	24.07-31.10 (10)	05.02-07.07 (18)	6.8-7.4	3.8-6.5
LD24:0	745	1183	763	3529	13.05-31.12 (12)	16.03-12.07 (7)	5.2-9.4	3.5-7.8
L6	770	1363	736	3039	17.06-26.07 (6)	20.01-06.07 (14)	5.9-7.1	5.3-6.5
L9	755	1476	769	3658	20.06-30.09 (13)	18.02-23.06 (25)	5.7-8.8	3.6-5.7

3